

Fig. 20. *Exallonyx parvulus* new species. Stigma and cell in wing and flagellum of antenna.

Fig. 21. *Exallonyx grandis* new species. *a*, stigma and cell of wing; *b*, flagellum of antenna; *c*, petiole of abdomen; (*p*, propodeum; *t*, petiole; *z*, second abdominal segment).

THE RESPIRATORY SYSTEM OF THE CAROLINA LOCUST (*DISSOSTEIRA CAROLINA* LINNE).¹

BY STUART C. VINAL,

AMHERST, MASS.

This paper is one of a series of contributions from the Entomological Laboratory of the Massachusetts Agricultural College, dealing with the anatomy of the grasshopper, *Dissosteira carolina* L. In its preparation I have received much encouragement and assistance from Dr. H. T. Fernald, Dr. G. C. Crampton and Dr. W. S. Regan, and I would take this opportunity of expressing my appreciation of their kindly interest and advice.

HISTORICAL.

Aristotle (about 320 B.C.) propounded the theory that insects did not breathe, and it was not until the time of Malpighi (1669) that it was demonstrated that insects respire by means of internal tracheæ. The studies of Malpighi (1669) on the silk worm, of Swammerdam (1673) on the honey bee, and of Lyonet (1762) on the goat moth paved the way for later investigations, but the famous monograph of Straus-Durckheim (1828) on the anatomy of the cockchafer (*Melolontha vulgaris* L.) in which the tracheal system is treated in great detail, furnishes the basis for all modern work on the subject, such as that of Alt (1912) on the respiratory system of *Dytiscus marginalis* L., etc.

Among the works dealing with the respiratory system of Orthoptera in particular, may be mentioned the investigations of Marcel de Serres (1819) on *Truxalis nasutus*, Leon Dufour (1841) on the

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Anatomy of the Orthoptera, Hymenoptera and Neuroptera, and Miall and Denny (1886) on the cockroach. Packard (1878-1880) has given an excellent general description of the tracheal system of the red legged locust (*Mcclanoplus femur-rubrum* DeG.), but his work is lacking in detail, and contains many inaccuracies, due no doubt to the fact that the dissecting microscopes available at that time were but crude implements in comparison with the perfected binoculars of to-day and even with the help of our improved appliances and technique, the tracing out of the various ramifications of the tracheal system requires much time and patience. Snodgrass (1903) has apparently described the general features of the tracheal system in *Dissosteira*, but his paper is not accessible to me and but few copies of it were ever printed. Therefore, since no detailed account of the respiratory system of any primitive insect is at present generally available, the morphology of the tracheal system of *Dissosteira* has been worked out in the present paper to fill this lack.

ORGANS OF RESPIRATION.

A. External Organs or Spiracles. (Plate III, Fig. 4.)

Ten pairs of spiracles are present in *Dissosteira carolina*, two pairs of which are located on the sides of the thorax and eight pairs on the abdomen.

I. *Situation.* (Plate III, Fig. 4.)

The first thoracic spiracle (*I*) lies in the lateral intersegmental membranous region connecting the pro- and meso-thorax, and beneath the hind lobe of the pronotum.

The second thoracic spiracle (*II*) is situated just above the second coxal cavity between the meso- and meta-thorax.

The first abdominal spiracle (*III*) lies in the auditory cavity just anterior to the tympanal sense organ. The other seven pairs of abdominal spiracles (*IV* to *X*) are all similarly placed on the lower anterior margin of each dorsal plate to the ninth abdominal segment where no spiracles are present.

II. *Morphology.*

In the Carolina locust three types of spiracles are found.

(a) *First Thoracic Spiracle.*—(Plate IV, Fig. 11.) This is by far the largest spiracle in the body and is closed externally by a large

two-lobed valve. The basal portion of the anterior lobe is prolonged somewhat posteriorly, forming a protruding pocket of the body wall. The aperture immediately within the valve is divided into two chambers, each of which leads to a separate main tracheal tube. Between these tracheæ is a chitinous septum (*stm*) which arises at the inner side of the posterior valvular lobe and extends anteriorly. Here it is thickened on its free end to which an occlusor muscle (*ocm*) is attached. Two valvular muscles are connected to an internal chitinous projection which arises at the lower anterior corner of the forward lobe. One muscle is inserted at the thickened end of the septum (see Fig. 11) and is the true occlusor muscle, while the other runs to the outer edge of the posterior lobe. As mentioned above two separate main tracheal tubes arise directly from this spiracle as shown in figure 11. The dorsal or larger air tube supplies the cephalic tracheæ, while the lower or smaller tube gives off its branches to the thoracic muscles.

(b) *Second Thoracic Spiracle*.—(Plate IV, Fig. 12.) This consists of an external two-lobed valve, the anterior lobe of which is considerably larger than the posterior one, and leads directly into a single main tracheal tube. Each lobe is somewhat triangular in outline and their opposing corners are connected internally by a chitinous cross band. The occlusor muscle (*ocm*) is inserted at the middle of this band and extends ventrally to a chitinous projection of the integument. The contraction of this muscle draws both lobes together.

(c) *Abdominal Spiracles*.—(Plate IV, Fig. 13.) These differ markedly from the thoracic spiracles, their external orifice being permanently open and leading directly into a shallow oval cup which communicates with a single main trachea. The occluding apparatus is quite different from those described above and consists of an internal hinged lobe at the apex of which the occlusor muscle (*ocm*) is attached. The abdominal spiracles are partly surrounded by a peculiar semicircular horny margin which is merely the infolded edge of the integument surrounding the spiracle. The occluding lobe (left lobe, Fig. 13) is drawn down upon this horny margin by the occluding muscle (*ocm*), thus cutting off the supply of air to the tracheal tube.

Each of the eight pairs of abdominal spiracles is constructed on

the above plan, the first and last merely differing from the others in their larger size.

B. Tracheal System.

It is necessary to make a large number of dissections in order to obtain an accurate knowledge of this complicated system, for it is impossible by a single dissection to show all the tracheæ contained within the body.

In studying the tracheal system alcoholic specimens proved to be of very little value, as tracheæ filled with this fluid can be traced only with great difficulty. An attempt was made to fill the tracheæ with india ink, melted wax, and other substances, by submerging the insect in these materials and exhausting the air from the container, in the hope that atmospheric pressure would force these substances into the tracheæ when the air was again admitted, but these proved unsatisfactory. It was found that tracheæ containing air were very easily traced when dissected specimens were submerged in water, but this necessitated fresh insects.

After considerable experimentation the following method was devised for the preservation of locusts with air in their tracheæ.

The Carolina locusts were caught and killed in a cyanide bottle in the usual manner. At the close of a collecting trip these insects were placed in a desiccator on a wire gauze, the bottom part of which was partly filled with 8 per cent. formalin solution. This proved to be very satisfactory in preserving the air in the tracheal system and preventing the insects from hardening while the formalin gas liberated prevented molds and bacteria from breaking down the insect tissue.

I. Structure of the Tracheæ.

The tracheal system of insects originates in the embryo as tubular invaginations of the ectodermal layer, and therefore the fundamental structure is similar to that of the body wall. The tracheæ are elastic tubes lined by a chitinous layer corresponding to the chitinous exoskeleton of an insect, and are surrounded by an epithelial layer continuous with that of the hypodermis. The inner chitinous lining, called the intima, is thickened at regular intervals to form spiral threads, called tænidia, which are not continuous throughout the tracheal tube but are frequently broken. The tænidia function in

keeping the tracheæ permanently open without affecting their flexibility. These elastic threads are not found in the ultimate branches of the tracheæ, called tracheoles or in the air sacs.

II. *General Morphology of the Tracheal System.*

A detailed description of this system would require a very lengthy paper. It is therefore advisable to consider only the more important tracheæ found in the Carolina locust in the present article.

The tracheal system of the grasshopper may be divided into three distinct parts—

- (1) Cephalic tracheæ.
- (2) Thoracic tracheæ.
- (3) Abdominal tracheæ.

These will be treated separately in the following pages.

(a) *Cephalic Tracheæ.*

As we have seen, the first thoracic spiracle (Plate IV, Fig. 11) is composed of two chambers which give rise to two tracheal tubes. The upper chamber or larger opening leads into a large main tube which soon divides, forming two main tracheæ which run to the head. The dorsal branch, termed the superior cephalic trachea (Plate II, Fig. 1, I_1) runs to the dorsal surface of the head and joins the ophthalmic trachea (Plate III, Fig. 5; ot) surrounding the compound eye at the vertex (Plate IV, Fig. 10). The second branch, known as the median cephalic trachea, soon divides and sends a branch to the external lateral head muscles (Plate I, Fig. 5; I_{2a}). This also connects dorsally with the superior cephalic trachea and ventrally with the anterior tentorial arm plexus (Tp), as shown in Fig. 5. The other branch of the median cephalic trachea (Plate III, Fig. 1; I_{2b}) passes through the occipital foramen with the alimentary canal and divides, forming two branches at the main body of the tentorium. One branch (Fig. 1, I_{2b}') travels along the anterior edge of the dorsal tentorial arm giving off numerous small branches to the muscles and ends in a large air sac (A) situated over the alimentary canal (also see Plate IV, Fig. 14). The second branch of I_{2b} (Fig. 1, I_{2b}'') extends forward and gives off a small branch closely applied to the proventriculus while the main tube runs to the under surface of the brain. Here it forms a large number of vesicular air sacs, which completely surround this organ. Just before the

median cephalic trachea divides to form its two main tracheæ running to the head a ventral branch is given off which unites with the inferior thoraco-cephalic trachea (Plate III, Fig. 1; *tc*). The thoraco-cephalic trachea (*tc*) enters the head just beneath the body of the tentorium (see Fig. 1 and Fig. 14), then curves laterally, giving off branches to the labium, maxillæ, and mandibles, while the main tube continues on and ends at the plexus situated at the junction of the anterior tentorial arm and external chitin (Fig. 5).

The following tubes constitute the more important tracheæ found in the head region.

The ophthalmic trachea (Plate III, Fig. 5, *ot*) surrounding the compound eye gives off numerous branches which supply the optic ganglia. A large sac-like tube (*gt*) originates from the ventral portion of the ophthalmic trachea and runs ventrally beneath the gena to the anterior tentorial plexus (*Tp*) previously mentioned. Connecting these tentorial arm plexuses is a large transverse dilated trachea which passes in the front of the head just above the junction of the clypeus and frons (Fig. 6). From this tube, branches are given off to the clypeus and labrum. Medially this transverse tube gives off a dorsal dilated air sac which supplies the front of the head and connects dorsally with both the ophthalmic and superior cephalic tracheæ.

All the above mentioned tracheæ receive air through the large chamber of the first thoracic spiracle, with the exception of the thoraco-cephalic trachea which receives air from the first, second and third spiracles (*I, II, III*) in a more or less indirect manner.

(b) *Thoracic Tracheal System.*

The thorax contains many muscles all of which must be intimately supplied with oxygen. This necessitates a large number of tracheæ whose arrangement is very complicated. The tracing of this system becomes very difficult because upon removing a muscle to expose the tracheæ beneath, a large number of the connections between the tracheal tubes of each layer are destroyed.

The tracheæ situated in the median sagittal plane will be discussed first (Plate I, Fig. 1). The other figures (Fig. 2 and Fig. 3) are drawn looking from within and removing one muscle layer at a time until the last layer is reached, which is drawn both from within (Fig.

3) and by removing the external chitin of the thorax (Plate IV, Fig. 7).

In general, tracheal tubes originate at the lower or smaller chamber of the first thoracic spiracle and pass backward between the muscle layers to the first abdominal spiracle (*III*) and connect with the second spiracular plexus at the different intersections of this plexus and the muscle layers.

The tracheal system of the thorax is best understood if two divisions are discussed separately: (1) Dorsal tracheæ which supply air to most of the thoracic muscles, and (2) ventral tracheæ which supply the head, nervous system and legs.

Dorsal Thoracic Tracheæ.—The median sagittal section and its air tubes will be discussed first (Plate III, Fig. 1). From spiracle *III* a branch is given off which runs to the median surface of the dorsal longitudinal muscles (*III-Ba*), where it divides into three branches which distribute themselves over the surface of these muscles, but all connect anteriorly with the main thoracic air sac *B* while still in the metathorax. This is the largest air sac found in the body and runs contiguous to the median surface of the dorsal longitudinal muscles, giving off many branches to these muscles. Just below the phragma, dividing the meta- and meso-thorax, this important air sac gives off a branch, which runs transversely beneath the dorsal longitudinal muscles and forms a compound plexus (*II-p*), receiving branches of the thoracic tracheal system at the different muscle levels, and finally connecting with the second thoracic spiracle. Anteriorly another ventral branch is given off by air sac *B* which joins indirectly the smaller chamber of spiracle *I*. This completes the dorsal thoracic tracheæ shown in Fig. 1.

On the lateral surface of the dorsal longitudinal muscles two arched tracheæ are found supplying air to these muscles. These are only partly shown in Plate III, Fig. 2. One of these originates at spiracle *I* (*I-D*) and connects posteriorly with air sac *D*, situated just anterior to the phragma dividing the meso- and meta-thorax, which in turn is joined ventrally with plexus *II-p*. The lateral side of the longitudinal muscles of the metathorax is furnished by an arched tracheal tube which originates at *II-p* (Fig. 2, *II-III a*) and ends at spiracle *III*.

Upon removing the dorso-longitudinal muscles of Fig. 1 the tracheæ shown in Fig. 2 are exposed. From spiracle *I* two main tubes run contiguous to the dorso-ventral muscles of the mesothorax (*I-II b₁*, *I-II-b₂*) and each terminates at the second spiracular plexus *II-p*. A trachea *II-III-b₁* originates at *II-p* and runs dorsalward in the metathorax contiguous to the dorso-ventral muscles and continues over the dorsal edge of these muscles, connecting with a small air sac shown in Plate III, Fig. 3, *E*, which in turn is indirectly united with spiracle *III*.

Upon removing the dorso-ventral muscles shown in Fig. 2 the more complicated tracheal system shown in Fig. 3 is exposed. In general this consists of a single principal trachea, *I-II-c*, which connects spiracle *I* with *II-p* and a trachea *II-III-c*, which connects *II-p* with spiracle *III*. In the mesothorax *I-II-c* gives off a ventral tube which connects with the tube *g* shown in Fig. 1. At the middle of *II-III-c* the main meta-thoracic trachea of Fig. 2 (*II-III-b₁*) after passing through the air sac *E* joins the tracheal system of figure 3. Ventrally *II-III-c* gives off an air sac *F* which connects with the sub-ventral trachea *w* of Fig. 1. The other trachea which is given off ventrally by *II-III-c* supplies tracheoles to the muscles. At *III* (Fig. 3) is shown a tube (*tc*) which runs antero-ventrally and is the origin of the thoraco-cephalic trachea (*tc*, Fig. 1).

In Plate IV, Fig. 7, are shown the tracheæ which lie just under the layer of muscles shown in Plate I, Fig. 3, but these have been drawn by removing the exoskeleton of the thorax. In Fig. 3 the second spiracular plexus continues ventrally and connects with the main spiracular trachea, as shown in Plate II, Fig. 7. Another branch from air sac *D* also connects with this main tube. The air sacs shown in Fig. 7 will not be discussed, as reference to the figure will explain their significance in supplying air to the dorso-ventral muscles. From spiracle *II* a ventral branch is given off which soon divides, sending one branch into the mesothoracic leg (*I₂*), while the other branch is connected with air sac *C* of Fig. 1. From spiracle *III* a branch is sent into the hind leg (*I₃*), while another connects with the air sac *F*, the other side of which has been shown in Fig. 3. From the smaller chamber of spiracle *I* a trachea is given off which runs to the fore leg and another main branch which runs to the

superventral trachea *I-II-b₃* (Plate III, Fig. 1). The main spiracular trachea also runs dorsally, giving off a branch which gives rise to the tracheæ of each muscle layer.

Ventral Thoracic Tracheæ.—Thus far only the dorsal thoracic tracheæ have been considered, but all the important points connecting these two systems have been noted.

The main tube running antero-ventrally from spiracle *III* (Plate III, Fig. 3, *tc*) and continuing forward through the thorax (Fig. 1, *tc*) to the head is the thoraco-cephalic trachea. This tube extends along each side of the ventral nerve cord to which it gives off many branches. A superventral branch (*I-II-b₂*, Fig. 1) arising from spiracle *I* runs posteriorly, giving off a branch which forms an air sac *C* (Fig. 1), which in turn is almost directly connected with spiracle *II* (see Plate IV, Fig. 7, and Plate III, Fig. 3). Near this air sac another branch is given off (Fig. 1, *g*), which connects with the ventral mesothoracic trachea given off by *I-II-c* of Fig. 3. Other branches of this trachea run into the metathoracic muscles, where they repeatedly divide, while the main tube (*II-h₃*) continues on and enters the metathoracic leg. An anterior branch is given off near air sac *C*, which supplies air to the salivary glands located in the mesothorax. An air tube *w* (Fig. 1), which arises from the lateral spiracular trachea of the abdomen between spiracles *III* and *IV*, runs forward and joins with air sac *F* (Plate III, Fig. 3).

(c) *Abdominal Tracheal System.*

In comparison with the cephalic and thoracic tracheal system that of the abdomen is simple. From each abdominal spiracle short air tubes connect with a main longitudinal spiracular trachea (*spt*, Fig. 8, and Fig. 9), which extends from spiracle *X* forward on each side of the abdomen to spiracle *III*. From this spiracular trachea originate all the branches found in the abdomen. Typically in each segment of the abdomen bearing a spiracle, three main tubes are given off by the spiracular trachea of that segment. One runs dorsally to connect with an undulating longitudinal dorsal trachea and soon after leaving the spiracular trachea gives off a branch which becomes distended, forming a large air sac which is connected with the air sac of both the preceding and following segments. A ventral branch is also given off by the main spiracular trachea which unites with the

ventral tracheal system. In addition to the dorsal and ventral branches a median tube is given off which supplies the alimentary canal with its tracheæ.

In describing the abdominal tracheal system three main divisions are recognized: (1) Dorsal, (2) ventral, and (3) alimentary tracheæ.

Dorsal Abdominal Tracheæ.—(Plate IV, Fig. 8.) In each segment of the abdomen bearing a spiracle, a dorsal branch, the dorso-segmental trachea, is given off by the main spiracular trachea. These branches connect dorsally with a right and left dorsal abdominal trachea (*da*), which runs in close approximation to the alary muscles of the heart. The dorsal abdominal trachea extends from spiracle *III* to beyond spiracle *X*, the latter spiracle being connected with this tube by three dorsal segmental tracheæ instead of one. The right and left dorsal abdominal tracheæ are independent and are in no way connected by transverse tubes.

The abdominal air sacs are closely associated with both the dorsal and alimentary tracheal systems. There are eight of these sacs on each side which originate as branches of the dorso-segmental tracheæ and those of each side are all connected by a longitudinal trachea which runs along the top of the alimentary canal and reproductive organs. These are usually found imbedded in the fat body. Over the ileum in the sixth abdominal segment the right and left longitudinal trachea connecting the air sacs unite to form the ileal plexus (*Ip*). The air sacs arising from spiracles *IX* and *X* join directly with this plexus as shown in Fig. 8.

Ventral Abdominal Tracheæ.—(Plate IV, Figs. 8 and 9.) In the dorsal abdominal tracheal system the two dorsal abdominal tracheæ run contiguous to the alary muscles of the heart, but are in no way connected with each other. In the ventral system a single ventral segmental tube is given off by the spiracular trachea in every segment bearing a spiracle. This segmental tube runs ventrally to join a ventral abdominal trachea (*va*), situated on each side of the nerve cord in every segment bearing a spiracle. Instead of the right and left ventral abdominal trachea being separate they are joined by a transverse tube which runs beneath the nervous system. This ventral system gives off many branches to the nerve cord and at its posterior extremity these tracheæ give rise to branches which supply

the genital organs (*x*). Anteriorly this system ends in small air sacs situated in the first abdominal segment.

Alimentary Canal Tracheal System.—(Plate V, Fig. 16.) With the exception of a short branch of *I 2b*" (Plate III, Fig. 1), which is contiguous to the proventriculus, all of the tracheal tubes connecting with the alimentary canal arise from the abdominal spiracles. From spiracle 3 two air tubes run to the alimentary canal, one connecting with the lateral alimentary trachea (*lr*), the other connecting with the superior alimentary trachea (*sp*). These longitudinal tubes, the lateral and superior alimentary tracheæ, are situated between the coecal pouches and are continued posteriorly in a more or less indefinite manner until opposite spiracle 8, where they unite to form a single tube which connects with spiracle 10. The superior alimentary trachea gives off many branches between its connections with spiracles 6 and 8, which enter the reproductive organs. The two branches given off by spiracle 3 supply the dorsal and lateral sides of the alimentary canal in the vicinity of the cœca, while the single branch given off from spiracle 4 supplies only the ventral portion of this region. From spiracles 5, 6, 7 and 8 two branches are sent to the alimentary canal, one, a dorsal tube connecting with the superior alimentary trachea (*sp*), the other a ventral branch supplying the ventral side of this canal. Spiracle 9 supplies a ventral tube running beneath the ileum, and a dorsal dilated tube which connects with the ileal plexus (*Ip*). From spiracle 10 many branches arise which supply tracheæ to the digestive canal and to the muscles of the reproductive organs. The most important trachea given off by this spiracle is a dilated tube which connects with the ileal plexus (*Ip*).

In Plate V, Fig. 16, the alimentary tracheal system has been drawn only for the left side. On the right side the air sacs which occur in the abdomen have been figured. These are also shown in Plate IV, Fig. 8.

The air sacs on each side of the abdomen are connected by a longitudinal tube which joins posteriorly the ileal plexus (*Ip*). This plexus, then, consists of six more or less dilated tubes which unite just anterior to the rectum and above the ileum.

In Fig. 16 only the right half of the rectum has been drawn in order that the origin of the tracheæ which appear on it may be better shown on the left side.

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TERMINOLOGY.

Spiracle Terminology.

I—First thoracic spiracle.

II—Second thoracic spiracle.

III—First abdominal spiracle.

IV-X—Second to eighth abdominal spiracles.

stm—Septum.

ocm—Occluding muscle.

In Fig. 16 Arabic numerals (3 to 10) are used instead of Roman numerals to represent the spiracles.

Tracheal Terminology.

Air sacs.

A—Cephalic air sac.

B—Main thoracic air sac.

C—Air sac connecting with spiracle *II*.

D, E and *F*—Other air sacs found in thorax.

Tracheal Tubes.

(a) Head.

*I*₁—Superior cephalic trachea.

*I*₂ (*a* and *b*)—Median cephalic trachea and branches.

gt—Genal trachea.

ot—Ophthalmic trachea.

Fig. 1

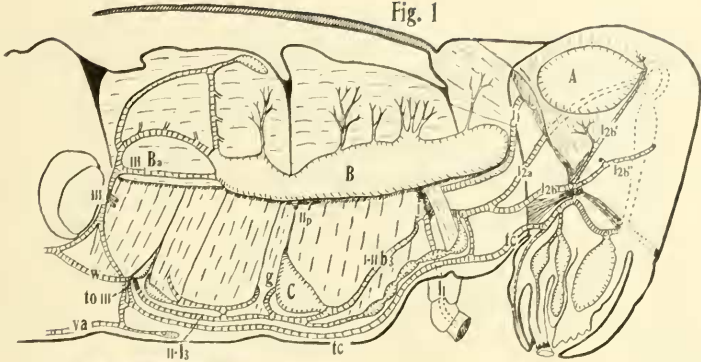


Fig. 2

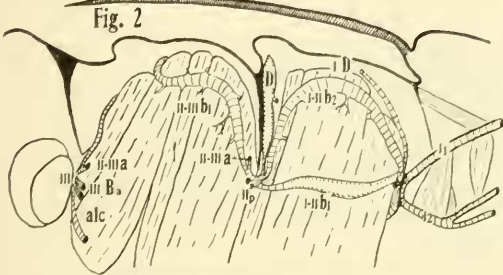


Fig. 3

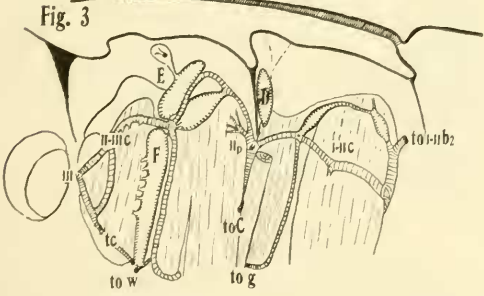


Fig. 5

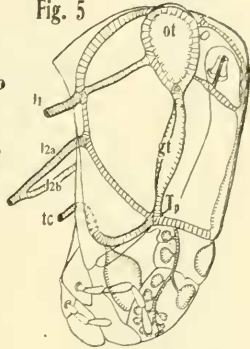


Fig. 4

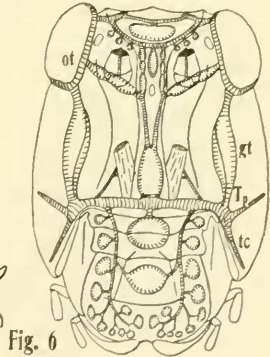


Fig. 6

Dissosteira carolina Lin.

